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ORIGINAL ARTICLE

Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*)

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Abstract When agonistic interventions are nepotistic, individuals are expected to side more often with kin but less often against kin in comparison with non-kin. As yet, however, few mammal studies have been in a position to test the validity of this assertion with respect to paternal relatedness. We therefore used molecular genetic kinship testing to assess whether adult female rhesus macaques (*Macaca mulatta*) from the free-ranging colony of Cayo Santiago (Puerto Rico) bias their interventions in ongoing dyadic aggressive interactions towards maternal and paternal half-sisters compared with unrelated females. It turned out that females supported maternal half-sisters significantly more often than paternal half-sisters or non-kin regardless of the costs associated with such interventions. Similarly, females targeted maternal half-sisters significantly less often than non-kin when this was associated with high costs. Unrelated females provided significantly higher mean rates of both high- and low-cost support to each other than did paternal half-sisters. However, females targeted paternal half-sisters significantly less often than non-kin when targeting was at low cost, suggesting that females refrain from intervening against paternal half-sisters. Our data confirm the general view that coalition formation in female mammals is a function of both the level of maternal relatedness and of the costs of intervention. The patterns of coalition formation among paternal kin were found to be more complex, and may also differ across species, but clear evidence for paternal kin discrimination was observed in female rhesus as predicted by kin selection theory.

Keywords Coalition formation · Paternal kin discrimination · Female rhesus macaques · Costs of intervention

Introduction

A coalition is formed when an individual intervenes in an ongoing conflict between two opponents to support one against the other (de Waal 1992). Because support in favour of one opponent simultaneously implies targeting the other, coalitions represent triadic interactions involving a support-

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er, a recipient and a target. Coalition formation has been observed in birds (Harcourt 1992; Heinsohn et al. 2000), carnivores (Waser et al. 1994; Engh et al. 2000, 2005; Wahaj et al. 2004; Packer et al. 1991; reviewed in Zabel et al. 1992), cetaceans (Connor et al. 1992, 1999; Krützen et al. 2004) and primates (Harcourt and de Waal 1992). In particular, the precise nature of coalition formation has been studied in various Cercopithecine primates, that is, macaques and baboons (e.g. Kurland 1977; Kaplan 1977, 1978; Massey 1977; Walters 1980; Bercovitch 1988; Noë and Sluijter 1995).

Kin selection theory predicts that relatedness influences social behaviour because animals preferentially interacting with kin increase their inclusive fitness (Hamilton 1964). In mammals, females are particular interesting with respect to kin bias. They predominantly remain in their natal groups, whereas males disperse (Pusey 1987). This implies that females frequently interact with both kin and non-kin (Greenwood 1980). Previous studies have shown that female mammals preferentially support maternal kin against maternally unrelated animals, for example, spotted hyenas (*Crocuta crocuta*; Wahaj et al. 2004), rhesus macaques (*Macaca mulatta*l; Kaplan 1977, 1978; Bernstein and Ehardt 1985), bonnet macaques (*Macaca radiate*; Silk 1982), Japanese macaques (*Macaca fuscata*; Chapais et al. 1997), savannah baboons (*Papio cynocephalus*; Silk et al. 2004), and that female primates, in particular, take high risks when supporting maternal kin against opponents of higher social rank than themselves, for example, rhesus macaques (Datta 1983a,b; Kaplan 1977; Bernstein and Ehardt 1985).

Studies of coalition formation have so far only distinguished between maternal kin and maternally unrelated individuals (Wahaj et al. 2004). However, the latter category of subjects comprises a substantial proportion of paternal kin when male reproduction is skewed, as has been demonstrated in a number of mammals, for example, Damaraland mole rats (*Cryptomys damarensis*; Cooney and Bennett 2000), banded mongooses (*Mungo mungo*; Cant 2000), fallow deer (*Dama dama*; Say et al. 2003), black rhinoceros (*Diceros bicornis*; Garnier et al. 2001), spotted hyenas (Engh et al. 2002), African lions (*Panthera leo*; Packer et al. 1991), bottlenose dolphins (*Tursiops truncates*; Krützen et al. 2004), humpback whales (*Megaptera novaeangliae*; Nielsen et al. 2001), savannah baboons (Altmann et al. 1996), toque macaques (*Macaca sinica*; Keane et al. 1997), rhesus macaques (Widdig et al. 2004), Mandrills (*Mandrillus sphinx*; Charpentier et al. 2005). To assess the full importance of kin bias for the evolution of coalition formation, paternal relatedness therefore has to be taken into account.

Whether animals recognize their paternal kin or not has been discussed for decades (e.g. Gouzoules and Gouzoules 1987; Walters 1987; Bernstein 1991), a debate fuelled by contradictory findings in captive primates (e.g. Wu et al. 1980; Fredrickson and Sackett 1984; Sackett and Fredrickson 1987; Welker et al. 1987; Erhart et al. 1997). However, paternal kin discrimination has been clearly shown to occur in a number of mammalian species, for example, Belding's ground squirrels (*Spermophilus beldingi*; Holmes 1986), golden hamsters (*Mesocricetus auratus*; Todrank et al. 1998) and spotted hyenas (Wahaj et al. 2004). Recent field studies in primates have further revealed that Cercopithecine females are also capable of discriminating between paternal half-sisters and unrelated females. Among rhesus macaques, adult females bias their affiliation towards paternal half-sisters compared with unrelated females (Widdig et al. 2001), a result that has also been found in adult female savannah baboons (Smith et al. 2003; Silk et al. 2006) and juvenile mandrills (Charpentier et al. 2006). Kin selection theory also predicts that paternal kin should direct less aggression towards each other than towards non-kin (Hamilton 1964). However, no evidence for this assertion has been found in the context of dyadic aggression between rhesus macaques (Widdig et al. 2002). Paternal half-sisters were found to direct dyadic aggression towards each other at the same rate as towards unrelated females (Widdig et al. 2002). Kin discrimination is therefore likely to be context-dependent (cf. Waldman et al. 1988; Keane 1990; Pfennig et al. 1993) when observed only in connection with specific behavioural patterns but not others. Ultimately, kin selection is dependent upon three factors: the degree of relatedness, the costs of interaction and the benefit of interaction. Therefore, one might expect kin discrimination to happen in a complicated, strongly context-dependent fashion.

Coalition formation is one of the most complex behaviours exhibited by social animals. The intervening animal ('supporter') is involved into two conflicting interactions: their cooperation with the opponent who receives the support ('recipient') and their aggression directed towards the other ('target'). To date, no primate study has addressed the question under which conditions and in which context females discriminate paternal kin from non-kin in triadic interactions. It has been argued that the observed bias of support towards maternal kin might have evolved as a by-product of the high level of spatial proximity shared by kin (Chapais 2001). However, animals in frequent proximity are also expected to target their kin more often for the very same reason. In contrast, if coalitions are indeed nepotistic, then both maternal and paternal half-sisters are expected to support each other more than non-kin and to target each other less than non-kin (Silk et al. 2004).

The decision of whom to support or target depends upon the costs and benefits associated with an intervention (e.g. Hamilton 1964; Chapais 1992; Widdig et al. 2000; Engh et al. 2005). It is generally assumed that the benefit of supporting kin is higher than that of supporting non-kin. If injuries have an effect on fitness, and if intervention against a higher-ranking individual involves a risk of retaliation and, therefore, injury (Ehardt and Bernstein 1992), then such interventions can be considered to be of high cost. In contrast, interventions against lower-ranking targets are less likely to entail retaliation (Ehardt and Bernstein 1992) and can therefore be considered to be of low cost. When the costs of providing support are high, kin can be expected to support each other more often than non-kin, whereas when the costs of targeting are high, kin are expected to target each other less often than non-kin (Hamilton 1964).

The main goal of the present study was to investigate whether adult female rhesus macaques discriminate between maternal half-sisters, paternal half-sisters and unrelated females during interventions in ongoing dyadic aggression, and whether the level of such an involvement is a function of the retaliation risk. We expected that females would support both maternal and paternal half-sisters more than unrelated females, particularly when support is of high cost. Likewise, we expected that females would target both maternal and paternal half-sisters less often than unrelated females, particularly when targeting is of high cost. Given the previously reported differences in terms of both affiliation and aggression bias (Widdig et al. 2001, 2002), we predicted that females would support and target their maternal half-sisters more than their paternal half-sisters, despite the fact that they share a similar proportion of their genes identical-by-descent.

Methods

Study population

We studied one troop (group R) of rhesus macaques residing on Cayo Santiago, a 15.2-ha island offshore of Puerto Rico, which is inhabited by approximately 800 rhesus macaques. All monkeys are direct descendants of the 400 founder animals captured in India in 1938 (Rawlins and Kessler 1986). Rhesus monkeys live in multi-male, multi-female groups which are characterised by female philopatry (Gouzoules and Gouzoules 1987) and male dispersal (Lindburg 1969; Colvin 1983). They breed on a seasonal basis (Drickamer 1974), with inter-birth intervals of approximately 1 year (Rawlins and Kessler 1986). The mating season on Cayo Santiago usually lasts from May to October followed by a birth season from November to April. The dates of birth and sex of all subjects were extracted from the demographic database of the Caribbean Primate Research Center (CPRC). The study population comprises social groups of representative size, bearing in mind that group size in wild rhesus macaques varies widely between 10 and 240 individuals (Seth and Seth 1986; Southwick et al. 1996). Although our study group, troop R, is rather large, it is best studied in terms of paternity. During our study, group R consisted of 91 females, 35 natal males and 46 non-natal males. Our study was confined to the patterns of coalition formation exhibited by those adult focal females (*N*=34) which had maternal half-sisters, paternal half-sisters and/or unrelated females in the troop. The study was restricted to females because females remain in their natal group and therefore interact with both kin and non-kin.

Paternity analyses

Gestation in rhesus macaques takes an average of 167 days (Silk et al. 1991), and male reproduction does not commence before the age of 3 years (Bercovitch et al. 2003). Therefore, any male 1,250 days older than, and residing on the island 200 days before, the birth of a given individual was considered a potential sire. Paternity was determined using 15 microsatellites (Nürnberg et al. 1998; Widdig 2002) with $\log_{10}$-likelihood ratios (LRs) for paternity vs non-relatedness calculated as previously described (Krawczak 1999). Paternity of a given individual was regarded as established when the putative sire had an LR in favour of paternity that was larger than 2 (corresponding to a standardised paternity probability >99%) and at least one unit larger than the LR of any other potential sire. Paternity can be discerned for 76 (84%) of the 91 females in the study group. For the remaining 15 females, DNA fingerprints (Epplen 1992) were used to rule out the presence of a paternal half-sister in group R during the behavioural observation period (Widdig 2002).

Behavioural definitions

A ‘coalition’ is defined as a triadic interaction (involving a supporter, a recipient and a target) in which the supporter intervenes in an ongoing conflict between the recipient and target so as to support the former against the latter (de Waal 1992). Such an intervention can occur either in favour of (‘supporting’) or against (‘targeting’) a maternal half-sister, a paternal half-sister or an unrelated female. To account for the costs of interventions, we distinguished between situations in which the intervener was of higher or lower rank than the target. For example, an intervener would provide high-cost support to a half-sister when targeting a higher-ranking opponent, but low-cost support when targeting a lower-ranking opponent.

Kin and age categories

We classified all 91 group R females into specific kin and age categories, defined each time from the perspective of a focal female. Females were classified as maternal half-sisters when they were born to the same mother but had different fathers (coefficient of relatedness, r=0.25). Females were classified as paternal half-sisters when they were born to different mothers but had the same father (r≥0.25, because mothers have a substantially higher probability of being related than fathers; de Ruiter and Geffen 1998). To control for the influence of maternal kinship upon behaviour, we confined our analysis to paternal half-sisters that were born to mothers from different matrilineal families (defined below). The number of full siblings (r=0.50) was too few to warrant treatment as a separate category (Widdig et al. 2002). Pairs of females were classified as unrelated (i.e. r~0.00) when they matched two criteria. First, they had to be born into different matrilineal families, where a 'family' consisted of the oldest surviving daughter (or granddaughter if the daughter was deceased) of a matrilineal founder together with at least three of her offspring (Widdig et al. 2001). Second, they had to be paternally unrelated, that is, they were neither paternal half-siblings nor descendants of paternal half-siblings (e.g. cousins, aunt–niece and second cousins). For most adult females, only information on one or two generations of the paternal lineage was available (i.e. the identity of the father and maternal grandfather). Therefore, the possibility of some individuals belonging to the same patriline could not be ruled out.

Rhesus macaques can be assigned to non-overlapping birth cohorts, although infants from the same cohort may differ in age by up to 6 months. Females can be born either into the same birth cohort (peers) or into different birth cohorts (non-peers). Female rhesus macaques almost always give birth to a single offspring (Bercovitch et al. 2002) so that maternal half-siblings are usually of a different age. Paternal half-siblings and unrelated females, in contrast, can be either of the same or of a different age. We have reported that both paternal relatedness and age proximity have an effect on affiliation (Widdig et al. 2001, 2002), but during the current study, interventions among peers rarely occurred. Hence, we controlled for age by limiting our analysis to pairs of females of different age (non-peers), including maternal half-sisters, which invariably were non-peers (MS-NP), paternal half-sisters that were non-peers (PS-NP) and non-kin females that were non-peers (NK-NP) (Widdig et al. 2001).

Behavioural data

A total of 958 focal observation hours were collected by A. W. between May and December 1997 (Widdig 2002; Widdig et al. 2001, 2002). All group members were recognised on an individual basis. Data on coalition formation among the 34 focal adult females were based upon focal animal and all occurrence samplings (Altmann 1974; Martin and Bateson 1986). We combined focal and all occurrence data to increase the number of coalitions observed per female. Coalitions are relatively long-lasting, and often, noisy events (Altmann 1974) and rhesus macaques tend to redirect received aggression to lower-ranking individuals, often producing a series of conspicuous aggressive events (A. Widdig, personal observation). Therefore, the combination of all occurrence data with focal data was unlikely to substantially bias our results. We also collected focal and all occurrence data on dyadic aggression to (1) construct a dominance hierarchy of the adult females (see below) and (2) to assess the number of opportunities per female to support other females in the group. To calculate opportunities for intervention, we only used non-silent agonistic dyadic interactions (hereafter known as dyadic conflicts) defined as either non-silent aggression (e.g. vocal threat, lunge, charge, chase, bite and attack) or non-silent responses to aggression (e.g. scream). Silent agonistic interactions (e.g. open-mouth threat, head-bobbing and displacement) were excluded because these can have easily gone unnoticed by potential interveners.

We distinguished between high- and low-cost opportunities for intervention. Assume that an observed dyadic conflict involved two opponents (female X and female Y), with focal female Z supporting X while targeting Y. The intervention would have been deemed 'high cost' when Z was lower-ranking than Y and 'low cost' when Z was higher-ranking than Y. We excluded the information as to who initiated the original dyadic conflict because a potential intervener might have lacked this information. For each intervention in an ongoing dyadic conflict, we collected the following information whenever possible: (1) the identity of the aggressor and victim in the original dyadic conflict, (2) the kind and context of the aggression in the original dyadic conflict, (3) the identity of the intervener and (4) the sequence of the intervening individuals. In cases where more than one supporter was observed to intervene in the same dyadic conflict (polyadic support), the event was divided into several triads, including the same target and recipient, but different supporters (Widdig et al. 2000).

Data analysis

The dominance rank of all group females (N=91) was determined from the outcome of dyadic agonistic interactions with other females. All mothers were found to be dominant over their daughters and, with the exception of two pairs, all maternal half-sisters can be ranked as predicted from their birth order. The hierarchy was stable over the course of the study (see Widdig 2002 for details).

The 34 focal females intervened in 1,063 triads, with an average of 1.1 interventions per observation hour. For the present analysis, we extracted those 299 triads in which a focal female intervened in favour of either a maternal half-sister (125 triads), a paternal half-sister (16 triads) or an unrelated female (158 triads). We also extracted 363 triads in which a focal female intervened either against a maternal half-sister (33 triads), a paternal half-sister (11 triads) or an unrelated female (319 triads). To assess the level of kin bias, rates of support or targeting per opportunity to intervene were calculated for each focal female in all kin and cost categories. The observed number of low- or high-cost interventions by a given focal female in favour of, or against, another specific female was then divided by the number of low- or high-cost opportunities for potential intervention based upon the dyadic conflicts observed (cf. Widdig et al. 2000; Silk et al. 2004). For each focal female, the unit of analysis was thus the mean rate of intervention per opportunity to intervene towards or against a given age and kin category. These rates were compared between different kin categories using a Wilcoxon test.

To account for rank and age information simultaneously, we also performed a logistic regression analysis for dyads (supporter–recipient or supporter–target) using the absolute rank and age differences as independent variables. For each kin and cost category, we used a binary approach in which a dyad was coded as one if at least one support or targeting event was observed, and as zero otherwise.

Statistical tests

All statistical tests were conducted at a significance level of 0.05. Although we have coined directional hypotheses about the influence of kinship upon behaviour throughout (e.g. a particular kin category gives more support than another), the rationale of these predictions may potentially still be questioned. Therefore, we have chosen to use two-tailed statistical tests in all instances of formal significance assessment. Multiple testing was corrected for using the Dunn–Šidák method (Sokal and Rohlf 1995). An individual significance level alpha$_p$ (α_p) was calculated for each P value. Only P values less than or equal to α_p were held to indicate a significant test result to ensure an error rate of 0.05 in the entire test series. All analyses were carried out using SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

Results

We analysed the distribution of interventions by adult females either in favour of, or against, a specific non-peer kin category using the mean rates of high- and low-cost intervention per opportunity to intervene (Table 1). Females supported their maternal half-sisters significantly more often than unrelated females both at high and low cost (Table 2a,b). Our data also suggest a significant bias of high- and low-cost support of maternal half-sisters in comparison with paternal half-sisters (Table 2c,d). Females provided significantly more high- and low-cost support to unrelated females than to paternal half-sisters (Table 2e,f), a pattern contradicting expectation.

Females targeted their maternal half-sisters significantly less often than unrelated females at high costs (Table 3a) but not at low costs (Table 3b). Maternal half-sisters targeted each other significantly more often than paternal half-sisters at low cost (Table 3d) but not at high costs (Table 3c). Paternal half-sisters targeted each other significantly less often than unrelated females at low (Table 3f) but not at high costs (Table 3e).

Absolute rank and age difference explained some of the variation in the patterns of support and targeting. A significant impact of age difference was found upon both low- and high-cost support among maternal half-sisters. Rank differences were irrelevant because ranks are similar among maternal half-sisters owing to the maternal inheritance of ranks in Cercopithecines (Table 4). Among paternal half-sisters, neither rank nor age difference contributed significantly to support or targeting (Table 4). In contrast, the absolute rank difference was important for both high- and low-cost support observed between unrelated females, with an additional effect of age difference for low-cost support. With respect to targeting, we observed a significant effect of rank difference among non-kin at low cost (Table 4).

Table 1 Mean rates (±SD) of agonistic intervention in different kin categories

Kin category	*N*	High-cost support	Low-cost support	High-cost targeting	Low-cost targeting
MS-NP	34	0.0410±0.0499	0.0447±0.0723	0.0004±0.0022	0.0179±0.0329
PS-NP	19	0.0004±0.0017	0.0006±0.0017	0.0011±0.0044	0.0026±0.0058
NK-NP	34	0.0020±0.0040	0.0017±0.0018	0.0006±0.0007	0.0095±0.0166

In a given kin category, individual-specific rates were calculated dividing the observed number of high-cost interventions by a female by the respective number of high-cost opportunities of that female to intervene.

N Number of individuals analysed (*N*<34 reflects that some adult females were lacking partners in the respective kin category); *MS-NP* maternal half-sisters being non-peers; *PS-NP* paternal half-sister being non-peers; *NK-NP* non-kin female being non-peers

Table 2 Testing kin bias according to the costs of support

Prediction	N	Wilcoxon test (z)	P and α_p	Prediction supported?
MS-NP vs NK-NP				
a. MS-NP give more high-cost support than NK-NP	34	−4.742	$P<0.001$, $\alpha_p=0.017$	Yes
b. MS-NP give more low-cost support than NK-NP	34	−4.263	$P<0.001$, $\alpha_p=0.017$	Yes
MS-NP vs PS-NP				
c. MS-NP give more high-cost support than PS-NP	19	−3.297	$P<0.001$, $\alpha_p=0.025$	Yes
d. MS-NP give more low-cost support than PS-NP	19	−3.351	$P<0.001$, $\alpha_p=0.025$	Yes
PS-NP vs NK-NP				
e. PS-NP give more high-cost support than NK-NP	19	−2.480	$P=0.013$, $\alpha_p=0.050$	No[a]
f. PS-NP give more low-cost support than NK-NP	19	−1.965	$P=0.049$, $\alpha_p=0.050$	No[a]

Predictions of high- and low-cost interventions were tested using the Wilcoxon test. For abbreviations of kin categories, see Table 1. Multiple testing was corrected for using the Dunn–Šidák method, including all three different tests for the same behaviour (e.g. high-cost support). An individual significance level alpha$_p$ (α_p) was calculated for each P value. Only P values less than or equal to α_p were held to indicate a significant test result.

N Number of females tested in each comparison.

[a] This result is opposed to the prediction.

Discussion

The results of our study confirm previous findings that female mammals support maternal kin more often than maternally unrelated females (e.g. Wahaj et al. 2004; reviewed for primates in Chapais 1992, 2001; Silk 2002) regardless of the costs of support (Datta 1983a,b; Kaplan 1977; Bernstein and Ehardt 1985). The differences we observed in rhesus macaques between maternal and paternal half-sisters agree well with data on coalitions among spotted hyenas (Wahaj et al. 2004). However, they were not to be expected from kin selection theory because paternal half-siblings share a similar proportion of genes identical-by-descent, as do maternal half-sisters (de Ruiter and Geffen 1998). Nevertheless, a higher level of affiliation among maternal than among paternal half-sisters has already been suggested for different Cercopithecine species (Widdig et al. 2001; Silk et al. 2006; Charpentier et al. 2006) and for spotted hyenas (Wahaj et al. 2004). Our data further revealed that females target their maternal half-sisters significantly less often than unrelated females at high costs but not at low costs. The present study also corroborated earlier findings that females direct most (dyadic) aggression towards maternal half-sisters (e.g. Widdig et al. 2002) even when controlling for the greater spatial proximity of maternal half-sisters (Widdig 2002).

Coalition formation has been reported to occur between maternally unrelated mammals (Chapais et al. 1991;Noë 1992; Widdig et al. 2000; Silk et al. 2004), but these alliances might include a considerable number of paternal kin coalitions in species with a high skew in male reproductive success (see references in 'Introduction'). We therefore, for the first time, distinguished between paternal half-siblings and non-kin in the context of coalition formation among female primates. In contrast to previous primate studies, which reported stronger affiliation among paternal half-sisters than unrelated females (Widdig et al. 2001; Smith et al. 2003; Silk et al. 2006; Charpentier et al. 2006), our data provided no consistent evidence for a paternal kin bias in triadic interactions. Unrelated females supported each other significantly more often than did paternal half-sisters regardless of whether the costs of support were high or low. Our study further revealed that females in the study population target their paternal half-sisters significantly less often than unrelated females at low costs, which suggests that females refrain from targeting their paternal half-siblings in agonistic disputes. The lack of support among paternal half-sisters contradicts findings

Table 3 Testing kin bias according to the costs of targeting

Prediction	N	Wilcoxon test (z)	P and α_p	Prediction supported?
MS-NP vs NK-NP				
a. MS-NP targeting less at high costs than NK-NP	34	−3.797	$P<0.001$, $\alpha_p=0.017$	Yes
b. MS-NP targeting less at low costs than NK-NP	34	−0.393	$P=0.695$, $\alpha_p=0.050$	No
MS-NP vs PS-NP				
c. MS-NP targeting more at high costs than PS-NP	19	−1.342	$P=0.180$, $\alpha_p=0.050$	No
d. MS-NP targeting more at low costs than PS-NP	19	−2.411	$P=0.016$, $\alpha_p=0.017$	Yes
PS-NP vs NK-NP				
e. PS-NP targeting less at high costs than NK-NP	19	−1.569	$P=0.117$, $\alpha_p=0.025$	No
f. PS-NP targeting less at low costs than NK-NP	19	−2.243	$P=0.025$, $\alpha_p=0.025$	Yes

See details in Table 2.

Table 4 Binary logistic regression results for high- and low-cost support (or targeting, respectively) within dyads as a function of the absolute rank and age differences

Kin category	Variables tested	High-cost support	Low-cost support	High-cost targeting	Low-cost targeting
MS-NP	Abs rank	W=0.038, P=0.845	W=1.187, P=0.276	W=0.004, P=0.945	W=1.347, P=0.246
	Abs age	W=5.593, P=0.018	W= 5.914, P=0.015	W=0.004, P=0.953	W=0.232, P=0.630
PS-NP	Abs rank	W=1.477, P=0.224	W=2.820, P=0.093	W=0.009, P=0.923	W=2.409, P=0.121
	Abs age	W=0.016, P=0.899	W=0.396, P=0.529	W=0.030, P=0.864	W=0.045, P=0.831
NK-NP	Abs rank	W=20.904, P<0.001	W=11.968, P<0.001	W=1.160, P=0.282	W=14.696, P<0.001
	Abs age	W=0.040, P=0.841	W=21.365, P<0.001	W=1.898, P=0.168	W=2.728, P=0.099

The table shows the W and P values for each kin category for both high- and low-cost interventions.
Abs Absolute; *W* Wald statistic

made in spotted hyenas, which form more coalitions with paternal half-siblings than with unrelated individuals (Wahaj et al. 2004, see below). Nevertheless, the data of our study suggest that paternal kin discrimination influences coalition formation in female rhesus macaques, although explanations for the observed patterns would naturally remain speculative (see below).

The outcome of our study raises three questions. First, why is there a bias of support only towards maternal half-sisters when paternal half-sisters share a similar (or greater) amount of genes? Maternal half-sisters show a higher level of affiliation than paternal half-sisters in mammals (e.g. Widdig et al. 2001; Wahaj et al. 2004; Silk et al. 2006), so the bias of support towards maternal half-sisters would seem plausible. Support was preferentially given to similar-ranking females because maternal half-sisters are always adjacent in rank, whereas paternal half-sisters and unrelated females vary tremendously in rank difference (Widdig et al. 2001). Thus, support between maternal half-sisters may reflect the generally observed attraction between similar-ranking females (de Waal and Luttrell 1986; de Waal 1991; Chapais et al. 1991, 1994; Kapsalis and Berman 1996a,b). In 61% of all triads support between maternal half-sisters was given by the younger (and therefore higher-ranking) sister who no longer competed over rank with their older sisters. Hence, the different patterns observed among maternal and paternal relatives in terms of coalition formation suggest that kin selection per se is insufficient to account for the support and targeting interventions in this population.

The second question is why do maternal half-sisters also target each other most often? An earlier study on rhesus macaques indeed reported high levels of dyadic aggression between close maternal kin (Bernstein and Ehardt 1986), but female bonnet macaques have been shown to direct more severe aggression towards non-kin (Silk et al. 1981). Coalition patterns among adult female baboons also differ from those reported in the present article in that baboons target close kin less often than non-kin (Silk et al. 2004). The pronounced targeting of maternal half-sisters in our study can be the result of living in an extremely despotic society with strong kin bonding, a characteristic of rhesus macaques. Both positive and negative interactions are promoted when animals are frequently in close spatial proximity. Kin are both close competitors and associates (Alexander 1974; Chapais 1995), and competition among kin can reduce or eliminate the benefits of kin selection (West et al. 2002). Our study appears to highlight a conflict of interests for individual females because interventions against maternal half-sisters mostly targeted older (and therefore lower-ranking) sisters (97%) and often entailed the support of a more closely related female than the sister (e.g. their mother or own offspring) (61%). Our findings suggest an interaction between absolute age difference and the probability of giving support to maternal half-sisters, whereas the absolute rank difference does not cause differences in terms of intervention. Hence, age proximity not only influences aggression and affiliation among social partners (Widdig et al. 2001, 2002) but also mediates the process of coalition formation among maternal kin.

The final and most important question is why do female rhesus macaques tend to refrain from supporting paternal half-siblings? Our data do not provide an answer to this. One possible explanation might be that paternal kin face more serious constraints such as difference in rank with respect to their intervention capabilities than do maternal kin. However, unrelated females vary in rank similarly to paternal half-sisters (Widdig et al. 2001). The logistic regression analysis suggested that absolute rank and age differences do not contribute much to the willingness to support paternal half-sisters. Nevertheless, high-ranking females gave more support to both paternal half-sisters and unrelated females when compared with low-ranking females (data not presented). This might suggest that support, regardless of kinship, is expected mainly among high-ranking females because they have a greater opportunity at lower cost than low-ranking females to regulate social relationships within a group (Silk et al. 2004). Nevertheless, that females refrain from targeting their paternal half-siblings in agonistic disputes represents one form of nepotism.

In contrast to rhesus macaques, paternal half-siblings of spotted hyenas have been found to form more coalitions with each other than do unrelated individuals, to direct less dyadic aggression towards each other than towards unrelated individuals, but not to affiliate more than unrelated individuals (Wahaj et al. 2004). Although the observed differential interactions with kin and non-kin are in accordance with predictions made by kin selection theory (Hamilton 1964), the actual behavioural patterns in hyenas and primates point in opposite directions (affiliation: Widdig et al. 2001; Smith et al. 2003; Silk et al. 2006; Charpentier et al. 2006; dyadic aggression: Widdig et al. 2002; coalitionary support: this study). One possible explanation for this discrepancy might be rank difference. Thus, the study on spotted hyenas was matched for social rank (Wahaj et al. 2004), whereas in our sample, as in other primate studies, the rank difference between paternal half-sisters ranged from small to large. In fact, our own data suggest that paternal half-sisters support each other more when they are similar in rank (data not shown).

In summary, kin bias in coalition formation among adult female rhesus macaques seems to be nepotistic (cf. Chapais 2001). The reason why females affiliate more with paternal half-sisters than with non-kin, but do not provide paternal half-sisters with more support than non-kin, remains unknown. Similarly, it is still unclear why females target paternal half-sisters less often than non-kin in triadic aggression (this study) but not dyadic aggression (Widdig et al. 2002). Whether context-dependent kin discrimination is due to a lack of benefit in certain behavioural contexts or whether other constraints inhibit paternal kin bias remains to be answered by future studies. Although the observed differential interactions are in accordance with the predictions of kin selection theory (Hamilton 1964), it is likely that sociality and the concomitant patterns of competition and cooperation invoke a complex interplay that balances kinship against the costs and benefits of interactions.

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References

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Altmann J (1974) Observational study of behavior sampling methods. Behaviour 49:227–267

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW (1996) Behavior predicts genetic structure in a wild primate group. Proc Nat Acad Sci USA 93:5797–5801

Bercovitch FB (1988) Coalitions, cooperation and reproductive tactics among adult male baboons. Anim Behav 36:1198–1209

Bercovitch FB, Widdig A, Berard JD, Nürnberg P, Kessler MJ, Schmidtke J, Trefilov A, Krawczak M (2002) Multiple sirehood in free-ranging twin rhesus macaques, *Macaca mulatta*. Am J Primatol 57:31–34

Bercovitch FB, Widdig A, Trefilov A, Kessler MJ, Berard JD, Schmidtke J, Nürnberg P, Krawczak M (2003) A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. Naturwissenschaften 90:309–312

Bernstein IS (1991) The correlation between kinship and behaviour in non-human primates. In: Hepper PG (ed) Kin recognition. Cambridge University Press, Cambridge, pp 6–29

Bernstein IS, Ehardt CL (1985) Agonistic aiding: kinship, rank, age and sex influences. Am J Primatol 8:37–52

Bernstein IS, Ehardt CL (1986) The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). Anim Behav 34:739–747

Cant MA (2000) Social control of reproduction in banded mongooses. Anim Behav 59:147–158

Chapais B (1992) The role of alliances in social inheritance of rank among female primates. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 29–59

Chapais B (1995) Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. Yearb Phys Anthropol (Wash) 38:115–136

Chapais B (2001) Primate nepotism: what is the explanatory value of kin selection? Int J Primatol 22:203–229

Chapais B, Girad M, Primi G (1991) Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. Anim Behav 41:481–491

Chapais B, Prud'homme J, Teijeiro S (1994) Dominance competition among siblings in Japanese macaques: constraints on nepotism. Anim Behav 48:1335–1347

Chapais B, Gauthier C, Prud'homme J, Vasey P (1997) Relatedness threshold for nepotism in Japanese macaques. Anim Behav 53:1089–1101

Charpentier M, Peignot P, Hossaert-McKey M, Gimenez O, Setchell JM, Wickings EJ (2005) Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). Behav Ecol 16:614–623

Charpentier M, Peignot P, Hossaert-McKey M, Wickings EJ (2006) Kin recognition in juvenile mandrills (*Mandrillus sphinx*) Anim Behav (in press)

Colvin J (1983) Rank influences rhesus male peer relationship. In: Hinde RA (ed) Primate social relationship, an integrated approach. Blackwell, Oxford, pp 57–64

Cooney R, Bennett NC (2000) Inbreeding avoidance and reproductive skew in a cooperative mammal. Proc R Soc Lond B Biol Sci 267:801–806

Connor RC, Smolker RA, Richards AF (1992) Dolphin alliances and coalitions. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 415–443

Connor RC, Heithaus RM, Barre LM (1999) Superalliance of bottlenose dolphins. Nature 371:571–572

Datta SB (1983a) Relative power and the maintenance of dominance. In: Hinde RA (ed) Primate social relationship, an integrated approach. Blackwell, Oxford, pp 103–112

Datta SB (1983b) Patterns of agonistic interference. In: Hinde RA (ed) Primate social relationship, an integrated approach. Blackwell, Oxford, pp 289–297

de Ruiter JR, Geffen E (1998) Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). Proc R Soc Lond B Biol Sci 265:79–87

de Waal FBM (1991) Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. Anim Behav 41:383–395

de Waal FBM (1992) Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 233–257

de Waal FBM, Luttrell LM (1986) The similarity principle underlying social bonding among female rhesus monkeys. Folia Primatol (Basel) 46:215–234

Drickamer LC (1974) A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatol (Basel) 21:61–80

Ehardt CL, Bernstein IS (1992) Conflict intervention behaviour by adult male macaques: structural and functional aspects. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 83–111

Engh AL, Esch K, Smale L, Holekamp KE (2000) Mechanisms of maternal rank “inheritance” in spotted hyaena (*Crocuta crocuta*). Anim Behav 60:323–332

Engh AL, Funk SM, van Horn RC, Scribner KT, Bruford MW, Libants S, Szykman M, Smale L, Holekamp KE (2002) Reproductive skew among males in a female-dominated mammalian society. Behav Ecol 13:193–200

Engh AL, Siebert ER, Greenberg DA, Holekamp KE (2005) Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third-party relationships. Anim Behav 69:209–217

Epplen JT (1992) The methodology of multilocus DNA fingerprinting using radioactive or non-radioactive oligonucleotide probes specific for simple repeat motifs. In: Chrambach A, Dunn MJ, Radola BJ (eds) Advances in electrophoresis. VCH, Weinheim, pp 59–114

Erhart EM, Coelho AM, Bramblett CA (1997) Kin recognition by paternal half-siblings in captive *Papio cynocephalus*. Am J Primatol 43:147–157

Fredrickson WT, Sackett GP (1984) Kin preferences in primates (*Macaca nemestrina*): relatedness or familiarity? J Comp Psychol 98:29–34

Garnier JN, Bruford MW, Goossens B (2001) Mating system and reproductive skew in the black rhinoceros. Mol Ecol 10:2031–2041

Gouzoules S, Gouzoules H (1987) Kinship. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. The University of Chicago Press, Chicago, pp 299–305

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hamilton WD (1964) The genetical evolution of social behaviour I/II. J Theor Biol 7:1–52

Harcourt AH (1992) Coalitions and alliances: are primates more complex than non-primates? In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 445–471

Harcourt AH, de Waal FBM (eds) (1992) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford

Heinsohn R, Dunn P, Legge S, Double M (2000) Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. Proc R Soc Lond B Biol Sci 267:243–249

Holmes WG (1986) Identification of paternal half-siblings by captive Belding’s ground squirrels. Anim Behav 34:321–327

Kaplan JR (1977) Patterns of fight interference in free-ranging rhesus monkeys. Am J Phys Anthropol 47:279–288

Kaplan JR (1978) Fight interference and altruism in rhesus monkeys. Am J Phys Anthropol 49:241–250

Kapsalis E, Berman CM (1996a) Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). I. criteria for kinship. Behaviour 133:1209–1234

Kapsalis E, Berman CM (1996b) Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). II. Testing predictions for three hypothesized organizing principles. Behaviour 133:1235–1263

Keane B (1990) The effect of relatedness on reproductive success and mate choice in the white-footed mouse, *Peromyscus leucopus*. Anim Behav 39:264–273

Keane B, Dittus WPJ, Melnick DJ (1997) Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. Mol Ecol 6:267–282

Krawczak M (1999) Statistical inference from DNA evidence. In: Epplen JT, Lubjuhn T (eds) A laboratory guide to DNA fingerprinting/profiling. Birkhäuser, Basel, pp 229–244

Krützen M, Barré LM, Connor RC, Mann J, Sherwin WB (2004) ’O father: where art thou?’—Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, West Australia. Mol Ecol 13:1975–1990

Kurland JA (1977) Kin selection in Japanese monkeys. In: Contributions to primatology, vol 12. Karger, Basel

Lindburg DG (1969) Rhesus monkeys: mating season mobility of adult males. Science 166:1176–1178

Martin P, Bateson P (1986) Measuring behaviour. Cambridge University Press, Cambridge

Massey A (1977) Agonistic aids and kinship in a group of pigtail macaques. Behav Ecol Sociobiol l2:31–40

Nielsen R, Mattila DK, Clapham PJ, Palsboell PJ (2001) Statistical approaches to paternity analysis in natural populations and applications to the North Atlantic humpback whale. Genetics 157:1673–1682

Noë R (1992) Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 285–321

Noë R, Sluijter AA (1995) Which adult male savanna baboons form coalitions? Int J Primatol 16:77–105

Nürnberg P, Sauermann U, Kayser M, Lanfer C, Manns E, Widdig A, Berard J, Bercovitch FB, Kessler M, Schmidtke J, Krawczak M (1998) Paternity assessment in rhesus macaques (*Macaca mulatta*). Multilocus DNA fingerprinting and PCR marker typing. Am J Primatol 44:1–18

Packer C, Gilbert DA, Pusey AE, O’Brien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562–565

Pfennig DW, Reeve HK, Sherman PW (1993) Kin recognition and cannibalism in spadefoot toad tadpoles. Anim Behav 46:87–94

Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299

Rawlins RG, Kessler MJ (eds) (1986) The Cayo Santiago macaques. History, behavior and biology. State University of New York Press, Albany

Sackett GP, Fredrickson WT (1987) Social preferences by pigtailed macaques familiarity versus degree and type of kinship. Anim Behav 35:603–606

Say L, Naulty F, Hayden TJ (2003) Genetic and behavioral estimates of reproductive skew in male fallow deer. Mol Ecol 12:2793–2800

Seth PK, Seth S (1986) Ecology and behavior of rhesus monkeys in India. In: Else JG, Lee PC (eds) Primate Ecology and conservation, vol 2. Cambridge University Press, Cambridge, pp 192–305

Silk JB (1982) Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79:162–188

Silk JB (2002) Kin selection in primate groups. Int J Primatol 23:849–875

Silk JB, Samuels A, Rodman PS (1981) The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). Behaviour 78:111–137

Silk JB, Short J, Roberts J, Kusnitz J (1991) Gestation length in rhesus macaques (*Macaca mulatta*). Int J Primatol 14:95–104

Silk JB, Alberts SC, Altmann J (2004) Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim Behav 67:573–582

Silk JB, Alberts SC, Altmann J (2006) Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. Behav Ecol Socioiol (in press)

Smith KL, Alberts SC, Altmann J (2003) Wild female baboons bias their social behaviour towards paternal half-sisters. Proc R Soc Lond B Biol Sci 270:503–510

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Southwick CH, Yongzu Z, Haisheng J, Zhenhe L, Wenyuan Q (1996) Population ecology of rhesus macaques in tropical and temperate habitats in China. In: Fa JE, Lindburg DG (eds) Evolution and ecology of macaque societies. Cambridge University Press, Cambridge, pp 95–105

Todrank J, Heth G, Johnston RE (1998) Kin recognition in golden hamsters: evidence for kinship odour. Anim Behav 55:377–386

Wahaj SA, van Horn RC, van Horn TL, Dreyer R, Hilgris R, Schwarz J, Holekamp KE (2004) Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. Behav Ecol Sociobiol 56:237–247

Waldman B, Frumhoff PC, Sherman PW (1988) Problems of kin recognition. Trends Ecol Evol 3:8–13

Walters J (1980) Interventions and the development of dominance relationships in female baboons. Folia Primatol (Basel) 34:61–89

Walters JR (1987) Kin recognition in non-human primates. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. Wiley, Chichester, pp 359–393

Waser PM, Keane B, Creel SR, Elliott LF, Minchella DJ (1994) Possible male coalitions in a solitary mongoose. Anim Behav 47:289–294

Welker C, Schwibbe MH, Schäfer-Witt C, Visalberghi E (1987) Failure of kin recognition in *Macaca fascicularis*. Folia Primatol (Basel) 49:216–221

West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. Science 296:72–75

Widdig A (2002) Paternal kinship among adult female rhesus macaques (*Macaca mulatta*). Ph.D. thesis, Humboldt University Berlin. http://edoc.hu-berlin.de/dissertationen/widdig-anja-2002-07-17/

Widdig A, Streich WJ, Tembrock G (2000) Coalition formation among male Barbary macaques (*Macaca sylvanus*). Am J Primatol 50:37–51

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2001) Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proc Nat Acad Sci USA 98:13769–13773

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2002) Affiliation and aggression among adult female rhesus macaques: a genetic analysis of paternal cohorts. Behaviour 139:371–391

Widdig A, Bercovitch FB, Streich WJ, Nürnberg P, Krawczak M (2004) A longitudinal analysis of reproductive skew in male rhesus macaques. Proc R Soc Lond B Biol Sci 271:819–826

Wu HMH, Holmes WG, Medina SR, Sackett GP (1980) Kin preference in infant *Macaca nemestrina*. Nature 285:225–227

Zabel CJ, Glickman SE, Frank LG, Woodmansee KB, Keppel G (1992) Coalition formation in a colony of prepubertal spotted hyenas. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 113–135